Table 1. Plant species within areas of the Palo Verde marsh exposed to either high or low grazing intensities.

| Family | Growth Form | High grazing intensity | Low grazing intensity |
|---|---|---|---|
| Marantaceae | Upright aquatic herb | *Thalia geniculata* | *Thalia geniculata* |
| Poaceae | Grass | *Hymenachne amplexicaulis* | *Hymenachne amplexicaulis* |
| Cyperaceae | Reed | *Echinodorus andrieuxii* | - |
| Alismataceae | Upright aquatic herb | *Eleocharis elegans* | - |
| Nymphaceae | Water lily | *Nymphaea sp.* | - |
| Convolvulaceae | Vine | *Anisera martinicensis* | - |

maintain diversity (Connell 1978).

Structural diversity in the Palo Verde marsh increased along with richness in the high intensity grazing site. This site had a greater percentage of both low-lying vegetation such as water lilies (*Nymphaea* sp.) and open water, which represent preferred foraging habitat for *Jacana spinosa* and other aquatic bird species in the marsh (Mahar et al. this volume).

As a National Park, Palo Verde is ecologically, culturally, and economically important. Management strategies are the subject of continuing debate. If the primary management goal is to increase plant species richness of the marsh, then relatively higher grazing intensity is preferable. However, additional research will be needed to assess other effects of grazing in the marsh ecosystem, including potential impacts on nutrient cycling, the terrestrial habitats around the marsh, and other invertebrates and vertebrates that depend on marsh habitats.

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# Pseudobulb attributes and microhabitat characteristics of *Cyrtopodium paniculatum* (Orchidaceae) on limestone cliffs

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*Abstract:* The ground dwelling orchid, *Cyrtopodium paniculatum*, occurs on rocky limestone cliffs in Palo Verde National Park, Costa Rica. Plants in this environment face extreme spatial and temporal variation in availability of resources. *C. paniculatum* have pseudobulbs that apparently store water and nutrients. We quantified number of pseudobulbs, volume of pseudobulbs, and the proportion of sheathed pseudobulbs in the plant. We also measured soil depth, light levels, and the presence of other plants and litter, which were all hypothesized to influence resource stores of orchids. The number of pseudobulbs in a plant increased with soil depth and the mean volume of pseudobulbs was higher in the presence of litter while the proportion of sheathed pseudobulbs in a plant was lower in the presence of litter. Plant morphologies may offer a convenient measure of *C. paniculatum* resource stores and provide an indication of relative fitness among plants distributed across a patchy environment.

*Key Words: desiccation, orchid, resource storage, water stress*

## Introduction

Suitable microhabitat conditions, which can be scarce in harsh environments, may determine the relative fitness of individual plants. The limestone cliffs at the Palo Verde National Park, Costa Rica are one example of an inhospitable environment with patchily distributed resources, such as light, soil, and nutrients for the ground dwelling orchid *Cyrtopodium paniculatum*. On these cliffs, orchids may experience extremely different light levels depending on canopy cover and aspect of the slope. Therefore, microhabitat suitability may depend upon a light level that permits photosynthesis while limiting desiccation. In addition, soil is patchily distributed amidst a predominantly rocky terrain, and may also be a limiting resource for the orchid (because of its importance for nutrient availability and water retention). Nutrient availability and water retention may further depend on the structural complexity of root masses, which is likely to increase as more plants occupy a patch. Structural complexity may function to collect litter and retain soil, thereby maximizing the volume of soil, nutrients, and water available to orchids.

*C. paniculatum* plants have conspicuous swollen stem internodes, or pseudobulbs, that function as resource storage and a means for propogation and survival (Hunt 1973). The water and nutrients stored in pseudobulbs presumably reduce likelihood of plant mortality during the dry season when these resources become scarce (Dressler 1993). The fitness of a *C. paniculatum* plant may therefore be positively correlated with the number and volume of pseudobulbs. Furthermore, each plant contains a mixture of sheathed and unsheathed pseudobulbs. Based on the increased succulence of sheathed pseudobulbs relative to unsheathed pseudobulbs, we assumed that the unsheathed pseudobulbs were those currently being used by the orchid. If so, the proportion of sheathed pseudobulbs in a plant may indicate the quantity of stored resources relative to current demands.

We hypothesized that microhabitat characteristics, such as soil, light, and nutrient availability, would affect the resource stores of *C. paniculatum*, as indicated by the number and volume of pseudobulbs and the proportion of sheathed pseudobulbs in a plant. These measures are fitness indicators if, as we guess, resource stores influence the probability that an orchid will survive the dry season. We predicted that resource stores of orchids would increase with 1) greater soil depth, 2) greater light availability, 3) presence of other plants, and 4) presence of litter in the soil patch containing the orchid.

## Methods

On 13 - 14 Jan 2000, we examined all *C. paniculatum* plants that were within safe reach on the top of the limestone cliffs at the Mirador Guayacan, near the OTS field station, Palo Verde National Park, Costa Rica. An orchid plant was defined as a continuous, basally connected cluster of pseudobulbs. We measured the length (cm) of the plant as the greatest distance between two pseudobulbs and width (cm) at the midpoint of the plant length. For each plant, we measured the total number of pseudobulbs, the height and diameter of each individual sheathed pseudobulb (or a maximum of 10 randomly selected pseudobulbs when the number of sheathed pseudobulbs exceeded 10), and the total number of sheathed pseudobulbs. Pseudobulb volume was estimated as the volume of two cones, $v = \pi dh$. To quantify microhabitat conditions, we measured soil depth (cm) at the center of the plant and percent canopy cover (using a Model-A spherical densiometer). In addition, we recorded the presence or absence (categorical) of other plants and dead organic matter (chiefly litter) in the patch of soil occupied by each orchid.

We tested for relationships among measures of resource storage and microhabitat (correlation analyses for continuous variables and ANOVAs for categorical variables). We used stepwise regression analyses to evaluate the relative importance of different microhabitat characteristics for resource storage by orchids. We also evaluated all other possible linear models predicting pseudobulbs attributes from microhabitat variables for comparison with the model chosen by the stepwise regression algorithm (to test whether there were alternative models with comparable explanatory power).

## Results

Mean width and length of a plant was 42.5 cm (± 30.4 SD) by 60.7 cm (± 35.4 SD; n = 26). The total number of pseudobulbs, and length and diameter of sheathed pseudobulbs averaged 24.8 ± 19.1 pseudobulbs per plant, 33.3 ± 15.2 cm, and 3.6 ± 1.1 cm (mean ± SD). The proportion of sheathed pseudobulbs in a plant averaged 0.54 ± 0.20 (mean ± SD). Plants with more pseudobulbs tended to have a lower mean volume of sheathed pseudobulbs (Table 1). Plants with more pseudobulbs and a lower mean volume of sheathed pseudobulbs also tended to have an increased proportion of pseudobulbs that were sheathed (Table 1).

Table 1. Correlation matrix of continuous variables used in the stepwise multiple regression analyses. Response variables were number of pseudobulbs in a plant (No.), mean volume of pseudobulbs in a plant (Vol., in $cm^3$), proportion of sheathed to total pseudobulbs in a plant (S:T). Environmental variables were soil depth (cm) and percent canopy cover. N = 26 plants in 26 microhabitats.

| | No. | Vol. | S:T | Soil Depth | % Cover |
|---|---|---|---|---|---|
| No. | 1.00 | - | - | - | - |
| Vol. | -0.41 | 1.00 | - | - | - |
| S:T | 0.46 | -0.59 | 1.00 | - | - |
| Soil Depth | 0.42 | -0.26 | 0.12 | 1.00 | - |
| % Cover | -0.16 | -0.13 | 0.16 | 0.01 | 1.00 |

Soil depth and percent canopy cover averaged (mean ± SD) 10.9 ± 5.0 cm and 19.9 ± 9.6 %. Twelve of 26 orchid plants were growing in the presence of another plant and 16 of 26 were growing in the presence of litter. There were no significant relations among any of the environmental variables (Table 1; ANOVAs involving categorical variables not shown).





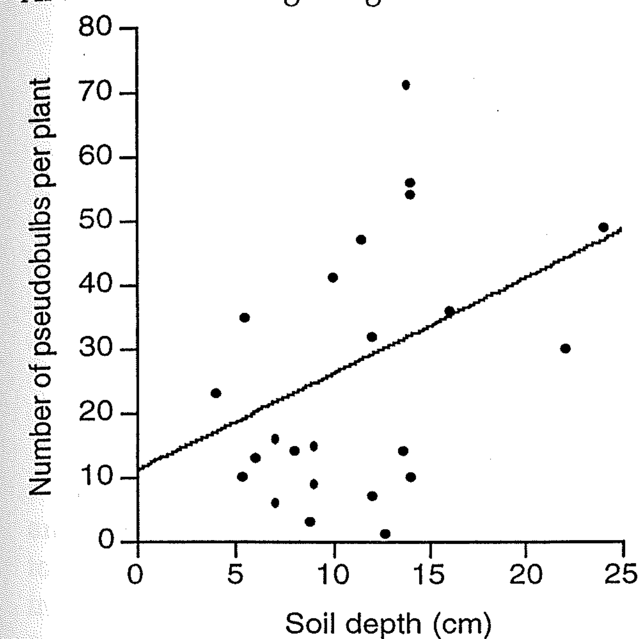


Figure 1. Relationship between soil depth and number of pseudobulbs per plant ($r^2 = 0.18$, $P = 0.037$).

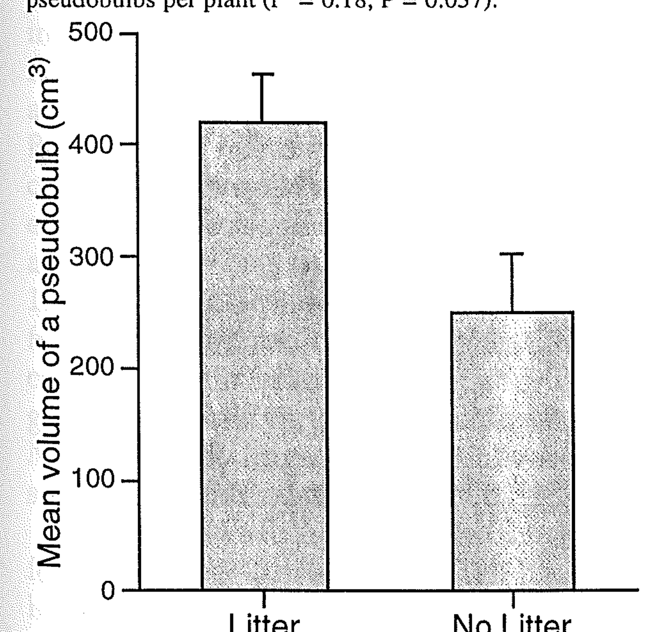


Figure 2. Mean volume (± SE) of a pseudobulb in a plant with the presence and absence of leaf litter.

Stepwise multiple regression analyses revealed a significant positive relationship between soil depth and the number of pseudobulbs in a plant (Fig. 1; Table 2). In contrast, litter presence was the best predictor of both mean pseudobulb volume and proportion sheathed to total pseudobulbs (Table 2). The mean volume of pseudobulbs was greater in the presence of litter than in the absence of litter (Fig. 2), and the proportion of sheathed to total pseudobulbs in a plant was lower in the presence of litter than in the absence of litter (Fig. 3). No other linear models relating environmental variables to pseudobulbs characters were significant ($p > 0.02$).

## Discussion

Positive relationships between (1) soil depth and the number of pseudobulbs and (2) the presence of litter and the mean volume of pseudobulbs in a plant suggest that resource stores, and perhaps fitness, of *C. paniculatum* depend on soil and litter conditions (Table 1). Depth of soil may make a site more suitable by increasing water retention and decreasing nutrient leaching. The presence of litter probably further increases water retention by adding to soil volume, and increases nutrient availability by providing organic nutrients that can be mineralized.

It is interesting that our different indicators of resource stores were related to different microhabitat variables. Different microhabitat characteristics might influence orchid fitness through different avenues. For example, increased soil depth may only permit space for the plant to produce more pseudobulbs. Presence of litter may result in a greater volume of pseudobulbs because orchids respond to high nutrients by growing larger pseudobulbs rather than more pseudobulbs.

Table 2. Results of stepwise regression analyses describing three measures of orchid resource stores (number of pseudobulbs in a plant, mean volume of pseudobulbs in a plant, and proportion of sheathed pseudobulbs in a plant) as a function of up to four environmental variables (soil depth, percent canopy cover, presence or absence of other plants, presence or absence of litter); p to enter/remove = 0.10. Only final models are shown.

| | F | p | $r^2$ |
|---|---|---|---|
| Y = Number of Pseudobulbs | | | |
| X = Soil Depth | 4.88 | 0.037 | 0.18 |
| Y = 7.68 + 1.62 X | | | |
| Y = Mean Volume of Pseudobulbs ($cm^3$) | | | |
| X = Presence of Litter (0 or 1) | 6.27 | 0.020 | 0.21 |
| Y = 334.66 - 85.22 X | | | |
| Y = Sheathed Pseudobulbs : Total Pseudobulbs | | | |
| X = Presence of Litter (0 or 1) | 4.98 | 0.035 | 0.17 |
| Y = 0.55 - 0.09 X | | | |

The proportion of sheathed pseudobulbs in a plant, our third measure of resource stores, was negatively related to the presence of litter. This runs counter to the apparently beneficial effects of litter as indicated by increases in mean pseudobulb volume. Because the rate at which an orchid plant uses the stored water and nutrients within a pseudobulb is unknown, it is possible that conditions early in the dry season necessitate faster use of stored resources. The proportion of sheathed pseudobulbs at this time of year may indicate current resource demands of the plant and not, as we initially guessed, resource stores that influence survival during the dry season.

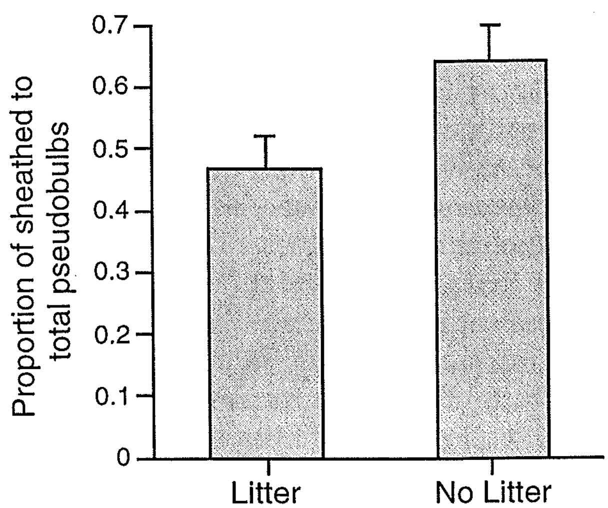


Figure 3. Mean proportion within plants (± SE) of sheathed to total pseudobulbs in the presence and absence of leaf litter.

This preliminary investigation of the ground dwelling orchid, *C. paniculatum*, revealed that soil depth and the presence of litter are related to resource stores as measured by number and mean volume of pseudobulbs in a plant. Microhabitat conditions may therefore influence orchid fitness within this population. Additionally, our study supports the use of pseudobulbs morphology as a surrogate of plant fitness when resources are patchily distributed.

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